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CREPIDULA CACHIMILLA (MOLLUSCA: GASTROPODA), A NEW SPECIES FROM PATAGONIA, ARGENTINA

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ABSTRACT

A new species, *Crepidula cachimilla*, is described based on a population from 15 m depth in San Antonio Oeste, Argentina. Shell length ranged from 5.4 to 28.5 mm for males and from 9.6 to 52.2 mm for females. The minimum shell length recorded for a brooding female was 23.5 mm, and the maximum shell length was 49.3 mm. A detailed anatomical description is given, showing as main characters of the species a relative thick columellar muscle, a greater closure of the pallial cavity aperture by a fusion of the mantle border, a very small osphradium, with about 16 broad filaments, endostyle divided by a middle longitudinal furrow, very large salivary glands, duplication of both gastric ducts to the digestive gland, male seminal vesicle very long and with irregular walls, pallial oviduct with a broad vaginal duct and a tall papilla originating both from pallial floor and roof. Brood egg masses of mature females contained from 15 to 65 egg capsules. The triangular-shaped egg capsules measured between 2.2 and 3.4 mm in length and between 2.3 and 3.8 mm in width. Each egg capsule contained between 129 and 563 eggs. The number of eggs per capsule and the egg diameter did not correlate with female shell length. Uncleaved eggs measured between 180 and 200 µm in diameter. They all developed synchronously within the egg capsules. Prehatching veliger shells measured between 260 and 300 µm in length. After hatching at the veliger stage, protoconch length during metamorphosis ranged between 700 and 800 µm. These parameters neither coincide with those reported by Hoagland (1977) for the similar Californian *Crepidula onyx*, nor with the reproductive characters reported by Miloslavich & Penchaszadeh (2001) for *Crepidula aplysioides*, which supposedly occurs in the region.

Key words: *Crepidula cachimilla*, new species, Calyptraeoidea, anatomy, reproduction, southwestern Atlantic, Patagonia, hermaphroditism.

INTRODUCTION

According to Dall (1909: 234), *Crepidula onyx* (G. B. Sowerby I, 1824) occurs along the Pacific coast from North America to Chile. Based on shell and radular morphology, Parodiz (1939) reported this species on the Atlantic coast of Argentina, from San Matías Gulf to Punta Norte, and Aguirre & Farinati (2000) recorded fossils of this species from the Quaternary period in northeastern Argentina. Hoagland (1977) suggested that the Atlantic material studied by Parodiz (1939) should be attributed to *C. aplysioides*. *Crepidula aplysioides* has been defined both anatomically (Simone, 2002) and by reproductive patterns (Miloslavich & Penchaszadeh, 2001). Based on the differences with the studied sample, we conclude that our material from San Antonio Oeste, Argentina, belongs to an undescribed species. In this paper, we describe this new species, which is restricted to an area of Patagonia, southwestern Atlantic.

The study on the calyptraeids has grown considerately in the last few years with the addition of knowledge on the anatomy (e.g., Simone, 2002), molecular biology (e.g., Collin, 2000), and reproductive strategies (e.g., Miloslavich & Penchaszadeh, 2001). From the eastern coast of Americas, knowledge of the informally defined "*Crepidula plana* complex" is of particular importance (Collin, 2000; Simone, submitted; Simone et al., 2000), of which this paper is a part.

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MATERIALS AND METHODS

Three samples were collected in March, May, and August 2001 at 15 m depth at Playa Orengo, San Antonio Oeste (40°53'S, 64°36'W), Argentina, by SCUBA diving. The animals were attached to the bivalves *Atrina seminuda* (d'Orbigny, 1846) and *Aulacomya atra* (Molina, 1782) and to stones. Approximately 370 specimens were collected.

Live individuals were carried to the laboratory, carefully detached from their substratum, measured to the nearest 0.1 mm precision with a digital vernier calliper, and some specimens dissected for anatomical description in vivo.

Shell parameters were measured following Hoagland's (1977) definitions. "D" refers to the length of the shell arc, whereas convexity is the relation between shell arc and shell length; "SL" refers to shell length.

The sexual characteristics of the population were determined by the presence or absence of a penis.

A total number of 47 egg masses was found and fixed in 5% seawater-formalin. Four randomly chosen egg capsules per egg mass were detached, and their length and width were measured under a stereomicroscope. Eggs and embryos contained within these egg capsules were counted and measured, and the presence or absence of cannibalism or nurse eggs was analyzed with a Kruskal-Wallis test.

Settlement size was estimated by measuring the protoconch length under SEM.

Simple linear regression type 2 following natural logarithmic (ln) transformations was carried out to identify the parameters of taxonomic value.

Radular characteristics of six individuals of different sizes were also studied with SEM.

The anatomical study was performed using standard methodology, with non-narcotized specimens fixed in 70% ETOH. Dissections were performed under a stereomicroscope, with the specimens immersed in fixative. All drawings were done with the aid of a camera lucida.

Abbreviations of anatomical structures are as follows: aa, anterior aorta; ab, auricle region beyond ventricle connection; ac, anterior extremity of gill on mantle border; ad, adrectal sinus; af, afferent gill vessel; ag, albumen gland; an, anus; ap, aperture of visceral vas deferens into pallial cavity; au, auricle; bg, buccal ganglion; ce, cerebro-pleural ganglia; cg, capsule gland; cm, columellar muscle; cv, ctenidial vein; dd, duct to digestive gland; dg, digestive gland; di, septum separating haemocoel from visceral mass; dm, dorsal shell muscle; dp, posterior duct to digestive gland; en, endostyle; es, esophagus; ey, eye; fd, foot dorsal surface; ff, female folds of genital papilla; fg, food groove; fl, female papilla; fp, female pore; gd, gonopericardial duct; gf, gastric fold; gi, gill; gp, pedal ganglion; gs, gastric shield; ig, probable ingesting gland; in, intestine; iu, "U"-shaped loop of intestine on pallial roof; ki, kidney; ll, left lateral expansion (flap) of neck; lm, lateral shell muscle; m1–m14, odontophore muscles; mb, mantle border; ml, mantle region restricting pallial cavity; mo, mouth; ne, nephrostome; ng, nephridial gland; nr, nerve ring; od, odontophore; os, osphradium; ov, pallial oviduct; oy, ovary; pb, proboscis; pc, pericardium; pd, penis sperm groove; pe, penis; pp, penis papilla; pr, propodium; py, pallial cavity; rg, repugnatorial gland; rl, right lateral expansion (flap) of neck; rn, radular nucleus; rs, radular sac; rt, rectum; sa, salivary gland duct; sd, pallial sperm groove; se, subesophageal ganglion; sg, salivary gland; si, siphon-like fold; sr, seminal receptacles; ss, style sac; st, stomach; su, supraesophageal glangion; sv, seminal vesicle; sy, statocyst; te, cephalic tentacle; tg, integument; tm, net of transversal muscles of haemocoel; ts, testis, ve, ventricle; vg, vaginal duct; vm, visceral mass; vo, visceral oviduct.

Abbreviations of institutions: AMNH, American Museum of Natural History, New York, New York, USA; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; MACN, Museo Argentino de Ciencias Naturales "B. Rivadavia", Buenos Aires, Argentina; MZSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.

RESULTS

Crepidula cachimilla, new species (Figs. 1–44)

Crepidula onyx Sowerby: Parodiz, 1939: 701, pl. 1, fig. 1; Scarabino, 1977: 185, pl. 3, fig. 5 (*non* G. B. Sowerby I, 1824).

Crepidula aplysioides Reeve: Hoagland, 1977: 369 (Argentinean material only) (*non* Reeve, 1859).

Type Material

Holotype: AMNH 306947. Paratypes: AMNH 306957 to 306961, 14 paratypes (5 dry specimens); AMNH 306948 to 306956, 9 paratypes

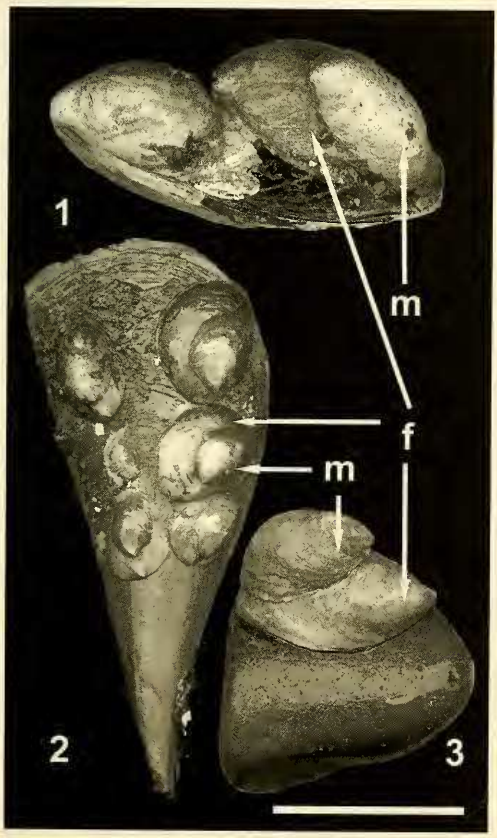
(4 females, 5 males preserved in ethanol); MZSP 41427 (15 paratypes); FMNH (10 paratypes).

Type Locality

Río Negro, San Antonio Oeste, Playa Orengo, Argentina (40°53'S, 64°36'W), 15 m depth, on shells of *Atrina seminuda* and *Aulacomya atra* and on stones (Figs. 1–3).

Etymology

The name of the species alludes to the mapuche word meaning great friend and is dedicated to our colleagues at the Invertebrates I Laboratory of the Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires.



FIGS. 1–3. *Crepidula cachimilla* on different substrata. FIG. 1: *Aulacomya atra*. FIG. 2: *Atrina seminuda*. FIG. 3: Rock. Scale bar = 3 cm. f: female; m: male.

Diagnosis

Shell outer surface smooth, lacking periostracum; apex projecting posteriorly, slightly away from posterior shell edge. Columellar muscle somewhat thick. Pallial cavity aperture restricted at right by a closure of mantle edge. Osphradium small, approximatgely 1/8 of mantle aperture length, with about 16–17 broad, closely spaced filaments. Endostyle divided by a middle longitudinal furrow. Hypobranchial gland greatly reduced. Transversal fold of kidney at level of nephrostome. Salivary glands very large, slightly larger than haemocoel. Both gastric ducts to digestive gland duplicated. Male seminal vesicle very large, coiled, wall markedly irregular. Female seminal receptacles reunited in a same region, mostly 4–5; vaginal duct long, broad; genital papilla tall, with a pair of separate longitudinal folds, ending subterminally.

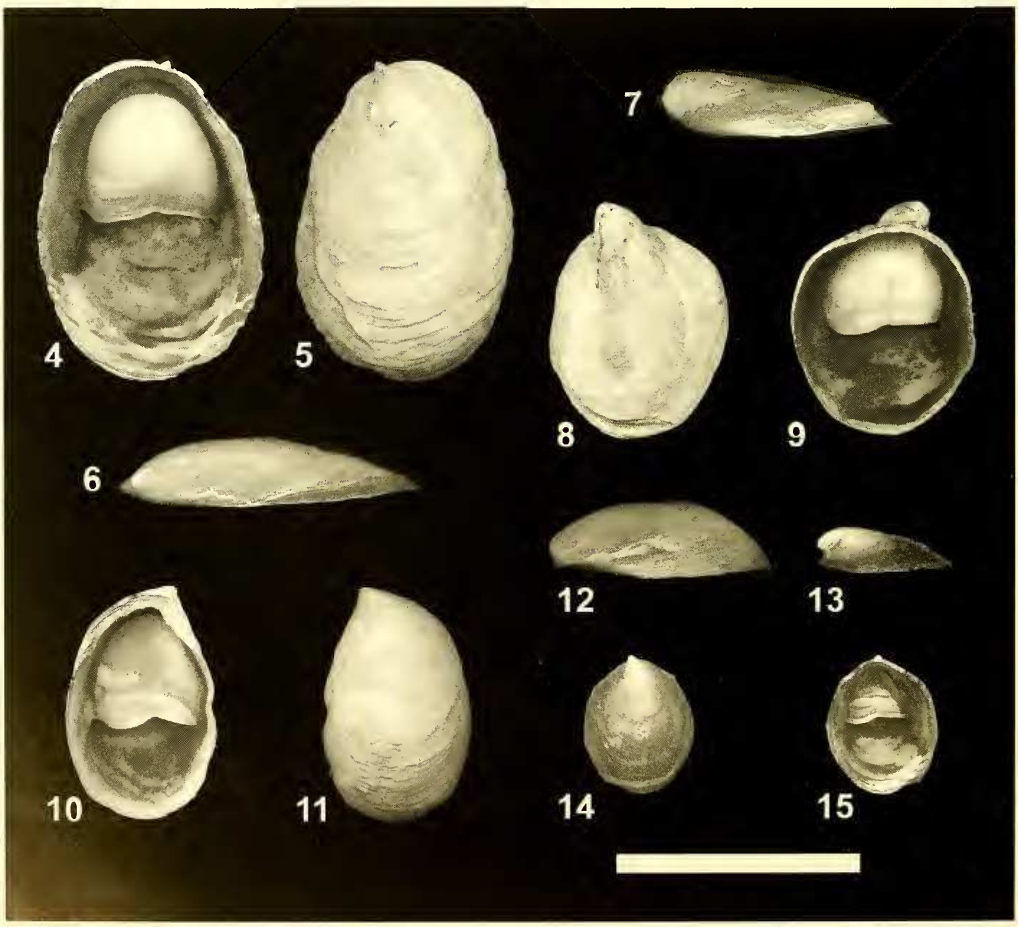
Description

Shell (Figs. 1–15): To 50 mm in length and 38 mm in width; walls with 0.46–0.60 mm thick; slightly to strongly convex (convexity = 1.095–1.350) (Table 1, including other measurements). Growth lines covering entire shell and septum. Color opaque-brown, internally bright-chocolate brown. In males, always opaque-brown externally and bright-brown internally. Few individuals (about 1%) with a white shell. Periostracum totally deciduous. Male specimens with very thin, brittle, flattened shells (Figs. 4–15). Protoconch smooth, with 1.4 whorls; transition to teleoconch not clearly defined. Aperture elliptical or subcircular. Apex solid, generally prominent, turned to right in females, almost central in males, slightly above margin, never reaching margin in males, extending beyond it in females. Flattened septum never convex, ridge central, margin with a clear central notch, covering less than half of ventral surface. Septal edge translucent, sinuous, slight turned towards right. Muscle scars inconspicuous.

Head-Foot (Figs. 16–18): Head differentiated, on long, dorsoventrally flattened neck, about half length of foot. Proboscis short, cylindrical. Tentacles long, stubby, apex somewhat bifid. Eyes dark, small, located on obsolete ommatophores in basal region of lateral margin of tentacles. Neck with pair of lateral, flattened lappets (nuchal lobes); left

expansion narrower than right; right expansion bringing low food groove along its dorsal limit with head (Fig. 17: fg). Foot very ample, occupying about 3/4 of shell concavity, dorsoventrally greatly flattened, thin; clear longitudinal inner sinus running in median line; shell septum as dorsal foot limit. Mantle fusing with dorsal surface of foot, protruding beyond its borders. Furrow of pedal glands transverse, in anterior margin of foot; anterior margin of foot covered dorsally by posterior region of neck ventral surface. Columellar muscle somewhat reduced, small, but somewhat thickened, contouring whole anterior border of shell septum, slightly taller at right (Figs. 17, 40: cm). Inner haemocoel cavity narrow, running approximately in center of neck region. Inner space almost filled by great quantity of transverse, very slender muscular fibers; these fibers connecting ventral surface of dorsal haemocoel wall with dorsal surface of its ventral wall, contouring salivary glands and esophagus (Fig. 18: tm). No vestiges of operculum except in very young specimens, being circular, paucispiral, thin, semi-transparent, flexible.

Mantle Organs (Figs. 16, 19–22): Mantle border thick, slightly hollow due to broad collar sinuses (Fig. 21). Mantle border surrounding entire shell ventral margin, free in anterior third, attaching to foot borders in posterior 2/3, situ-



FIGS. 4–15. *Crepidula cachimilla*. FIGS. 4–6: Female holotype, AMNH 306947. FIGS. 7–9: Female paratype 1, AMNH 306949. FIGS. 10–12: Female paratype 2, AMNH 306950. FIGS. 13–15: Male paratype 5, AMNH 306955. Scale bar for FIGS. 4–12 = 4 cm. Scale bar for FIGS. 13–15 = 2 cm.

ated slightly away from foot edge, connecting to it by a thin, semi-transparent portion. Mantle border without appendages, but entirely edged by series of minute repugnatorial glands, immersed in central region of mantle edge (Fig. 21: rg). Mantle border with special arrangement of folds in middle region of pallial cavity aperture, a somewhat narrow fold located from gill anterior end running towards left, decreasing and disappearing abruptly at level of osphradium, its broader region with a broad central furrow, its posterior edge expanding weakly beyond mantle border covering ventrally anterior region of gill, its anterior edge slightly projecting, but not extending beyond mantle edge (Figs. 19, 20, 22).

Dorsal shell muscle well developed (Fig. 16: dm), origin small, in about middle-right region of shell, just anterior to septum, its fibers running anteriorly, spraying like fan, inserting in adjacent anterior region of dorsal surface of pallial cavity. Lateral shell muscle (Figs. 16, 19, 20: lm) small, fan-like, located close to right side of mantle border, in region where pallial cavity penetrates shell septum chamber, with a differentiated muscular branch running towards mantle border, thickness restricting pallial aperture (Fig. 20). Pallial cavity aperture occupying about 2/3 of right-anterior half of shell border (compared to a clock in dorsal view, with head at 12 o'clock, pallial aperture from 11 to 2 o'clock) (Fig. 19); right region of pallial cavity aperture restricted by a broad closure of mantle border, forming a transverse septum (Fig. 20). Pallial cavity deep, broad, triangular, arched, dorsoventrally flattened. Anterior extremity of pallial cavity a little larger than its aperture because of closure in left and right extremities produced by fusion of mantle and foot (Figs. 19, 20: ml). Pallial cavity narrowing gradually towards posterior, penetrating at left of visceral mass; cavity length about 2/3 length of animal (Figs. 16, 19).

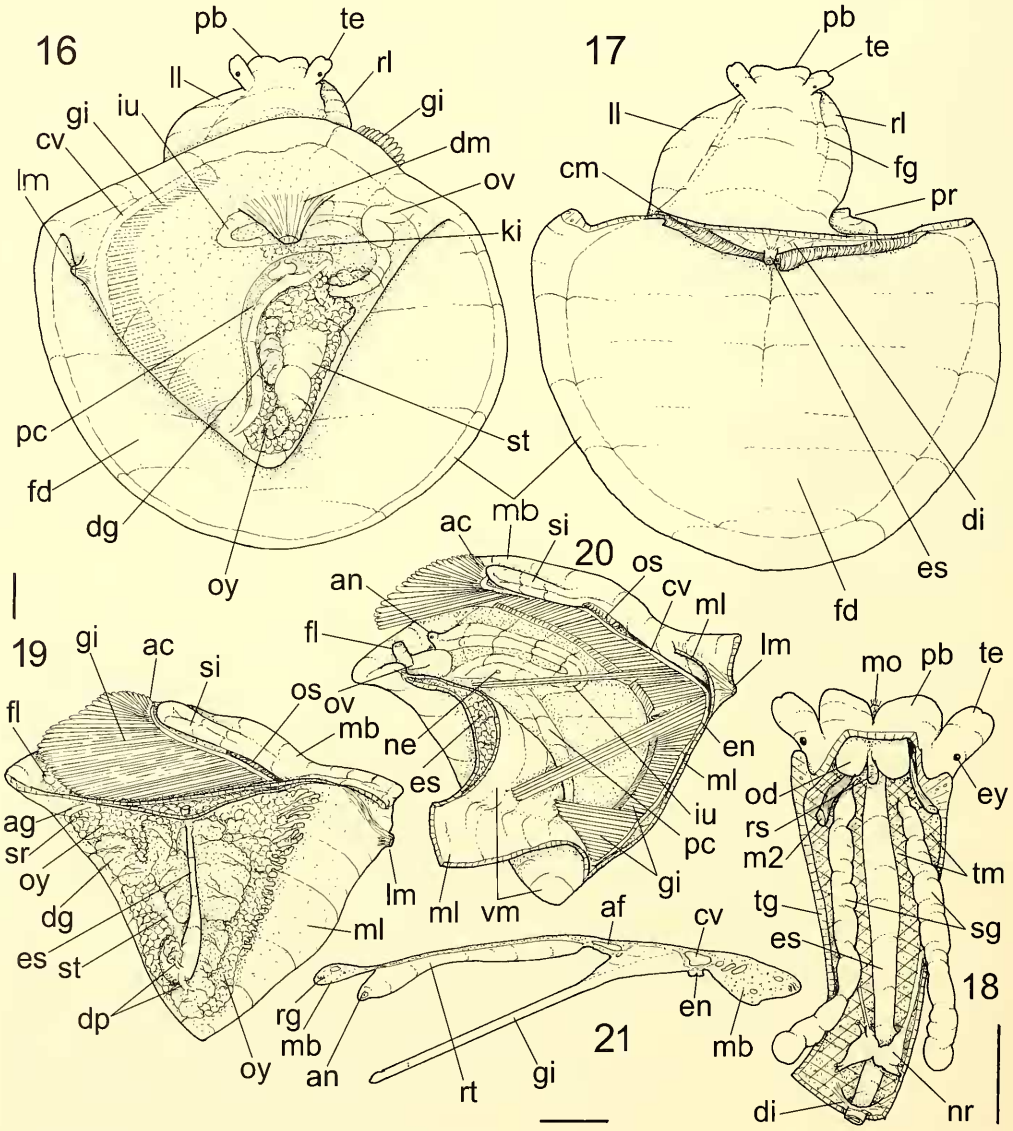
Osphradium small, monopectinate, located between anterior half of gill and mantle border, at some distance from gill anterior end, located about in left region of pallial aperture somewhat perpendicular to longitudinal axis of body (Figs. 19, 20). Osphradium length little more than 1/8 of pallial aperture length, in form of a small fold, attached to mantle, separated from gill structures. Osphradium leaflets cy-

TABLE 1. Measurements in mm of the holotype and paratypes.

Specimen	Total length (L)	Height	Width	D	Septum length	Septum free shell length	Convexity (D/L)
Holotype AMNH 306947 (female)	52.5	8.5	36.4	59.3	24.9	18.35	1.13
Paratype 1 AMNH 306948 (female)	30.9	8.4	21.8	35.4	12.2	16.1	1.14
Paratype 2 AMNH 306949 (female)	42.8	9.2	29.5	47.5	28.8	22.3	1.11
Paratype 3 AMNH 306950 (female)	38.7	7.8	27.4	41.3	11.3	19.1	1.07
Paratype 4 AMNH 306951 (female)	31.9	12.6	19.8	42.1	13.3	15.8	1.34
Paratype 5 AMNH 306952 (male)	20.1	6.4	14.7	23.8	8.8	9.3	1.18
Paratype 6 AMNH 306953 (male)	23.3	5.7	17.7	25.7	10.9	10.3	1.10
Paratype 7 AMNH 306954 (male)	15.3	3.7	11.6	17.2	5.8	8.3	1.12
Paratype 8 AMNH 306955 (male)	12.3	3.9	10.2	14.2	3.9	6.4	1.15
Paratype 9 AMNH 306956 (male)	26.6	8.2	20.2	30.9	12.1	13.3	1.16

lindrical, close from each other, somewhat thick, low, about 16–17 in number (Fig. 22: os) in females. Osphradium ganglion narrow.

Gill very large, its base narrow, edging anterior and left margin of pallial cavity almost the entirety of its length; anterior gill extremity in right-anterior region of pallial cavity aperture, near its right limit, on thick mantle border; gill posterior extremity in posterior end of pallial cavity (Fig. 20). Gill filaments triangular at their base and with very long, almost straight, narrow, stiff rod turned to right (Fig. 21: gi); rods



FIGS. 16–21. *Crepidula cachimilla* female anatomy. FIG. 16: Whole dorsal view, specimen extracted from shell. FIG. 17: Same, head-foot, dorsal view, visceral mass and pallial structures removed. FIG. 18: Head and haemocoel, ventral view, foot and neck "sole" removed. FIG. 19: Pallial cavity and visceral mass extracted, ventral view. FIG. 20: Same, left pallial connection sectioned, ventral portion of visceral mass deflected, most gill filaments artificially sectioned. FIG. 21: pallial cavity roof, transversal section in region tangent to rectum. Scales = 2 mm.

extending about three times longer than their triangular, membranous base; rods beginning in ctenidial vein region, in left margin of cavity roof, and touching food groove of head-foot, in right margin of cavity floor; rod apex rounded, preceded by thicker region. Gill filaments connected to each other by cilia, mainly in their thicker apical region, holding them in a somewhat firm position. Gill filaments longer in central gill region, shorting gradually in both extremities; gill anterior extremity with short filaments, abruptly turning forwards, located on mantle border (Fig. 22). Ctenidial vein narrow, with uniform width along its entire length. Endostyle well developed (Figs. 20, 21, 22: en), yellowish, in form of broad, flat glandular ridge located in middle level of ventral surface of ctenidial vein along its entire length. Endostyle divided longitudinally by a shallow middle furrow. Hypobranchial gland extremely thin, practically absent. About 1/3 of visceral mass encroaching on pallial cavity roof (Fig. 20), occupying about 1/3 of this cavity in posterior-right region; pericardium and kidney located posteriorly; a long intestinal loop, anus and pallial oviduct located anteriorly.

Visceral Mass (Figs. 16, 19, 20): Form of a dorsoventrally flattened cone, housed in shell chamber produced by septum, which separates visceral mass from dorsal surface of foot. Left and anterior region of visceral mass occupied by pallial cavity (Figs. 16, 19, 20). Remaining regions of visceral mass with stomach as central structure, immediately surrounded by greenish-beige digestive gland (except in some ventral and dorsal areas). Gonad surrounding digestive gland, more concentrated anteriorly and at left. Visceral mass encroaching on right-posterior region of pallial cavity roof, possessing another ventral flap as pallial cavity floor (Fig. 20: vm). Anterior extremity of visceral mass ventral flap ending at anterior border of shell septum, covering columellar muscle (Fig. 17).

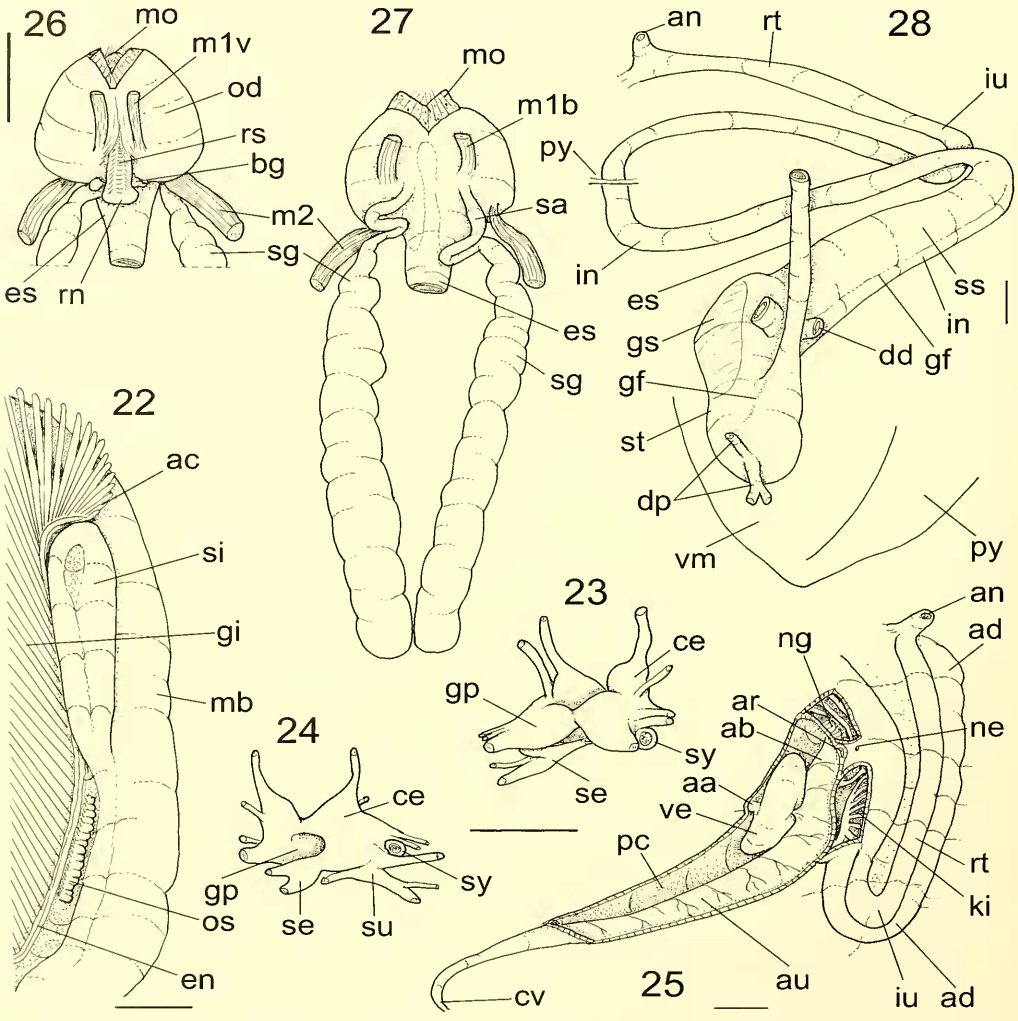
Circulatory and Excretory Systems (Figs. 20, 25): Pericardium somewhat triangular, broad, oblique to longitudinal axis of animal (Fig. 16: pc). Pericardium left region very narrow, in form of a vein connecting gill with auricle, beginning at posterior extremity of gill in posterior-left end of pallial cavity, running to surround area where visceral mass encroaches into pallial cavity, gradually increasing towards anterior and right (Fig. 25). Remaining pericardium limits: (1) anterior and ventral – pallial cavity; (2) posterior – visceral mass (gonad generally); (3) dorsal – mantle; (4) right – kidney. Auricle thin walled, long, narrow, running all along pericardium length, attached to its anterior and dorsal inner surfaces (Fig. 25), connecting with ventricle approximately in its middle portion; auricle having a broad portion beyond ventricle as blind sac (Fig. 25: ab), bearing orifice to nephridial gland. Ventricle elliptical, very muscular; its connection with auricle located about in middle region of its anterior surface, on opposite side bearing origin of aortas. Anterior aorta broad, running towards opposite side from posterior aorta. Anterior aorta running towards right, surrounding posterior inner pericardium surface, then penetrating head haemocoel.

Kidney occupying about half of area of visceral mass within pallial cavity (Fig. 20). Kidney limits: (1) dorsal – mantle; (2) ventral – pallial cavity; (3) posterior-right – visceral mass (gonad generally); (4) posterior-left – pericardium; (5) anterior – an intestinal loop; (6) lateral-right – intestine and oviduct (when present). Kidney central region hollow, with single anterior lobe (Fig. 25). Kidney lobe slightly uniform, covering dorsal surface, intestinal region passing through kidney chamber, and about 1/4 of inner space of kidney adjacent to intestine. Renal lobe having longitudinal, branching, narrow folds; a larger fold located at left of nephrostome having a series of anterior branches situated somewhat uniformly; another transversal, somewhat tall fold located at level of nephrostome. Nephridial gland in renal limit with pericardium, very small, having a series of triangular, transversal, narrow folds connected with dorsal renal lobe (Fig. 25: ng). Nephrostome a very small slit located in central region of ventral wall (Figs. 20, 25: ne), in anterior region of hollow portion of kidney; no inner glandular folds close to it. Adrectal sinus very broad, edging externally intestine loop exposed in pallial cavity, connected to main kidney chamber but separated by a thin septum (Figs. 20, 25: ad).

Digestive System (Figs. 16, 26–28): Proboscis short, broad (Figs. 16–18: pb). Pair of narrow ventral proboscis retractor muscles very thin, immersed in proboscis wall. Mouth longitudinal, in center of anterior proboscis surface. Buccal mass very large, occupying most of proboscis inner space and short portion of haemocoel posterior to it. Jaw plates in dorsal

wall of buccal mass thin, almost vestigial, broader laterally, short longitudinally. Pair of broad, low dorsal folds beginning well posterior to jaws; dorsal chamber between these folds shallow. Odontophore large, occupying most of buccal mass.

Odontophore muscles similar to other species of *Crepidula* (Simone, 2002) (Figs. 26, 27: m1); several very narrow jugal muscles connecting buccal mass with adjacent wall of snout, more concentrated anteriorly around mouth: m1b pair of dorsal protractor muscles narrow, thin, superficial, originating in anterodorsal region of mouth, close to median line, inserting in posterodorsal-lateral region of odontophore; m1v similar to m1b but located in ventral surface; m2 pair of retractor muscles of buccal mass (retractor of pharynx) broad,

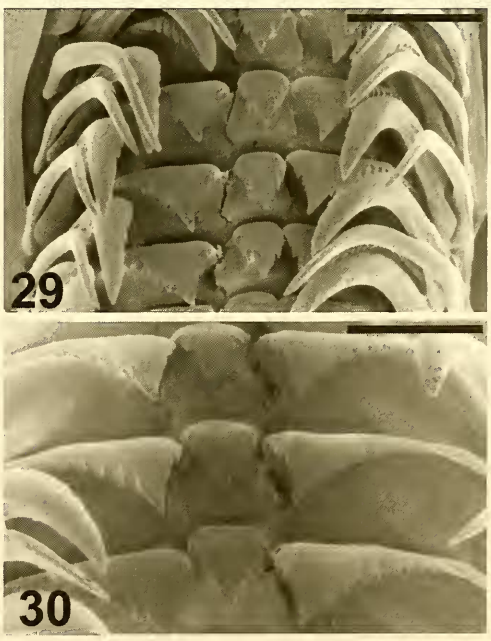


FIGS. 22–28. *Crepidula cachimilla* anatomy. FIG. 22: Anterior portion of pallial cavity, close to mantle border, mantle border slightly deflected for showing anterior gill region. FIG. 23: Central nervous system (nerve ring), ventral view. FIG. 24: Same, dorsal view. FIG. 25: Middle and posterior-right region of pallial roof, ventral view, ventral wall of pericardium and kidney partially removed. FIG. 26: Buccal mass, ventral view. FIG. 27: Same, dorsal view, salivary gland (sg) fully shown. FIG. 28: Middle and distal digestive tubes shown as in situ, ventral view, some adjacent structures also represented. Scales = 1 mm.

originating in lateral-ventral region of haemocoel just posterior to snout (Fig. 18), running towards anterior, inserting in lateral-posterodorsal region of odontophore cartilages; m2a pair of dorsal tensor muscles of radula, continuation of m2 after insertion in cartilages, running towards anterior, inserting in subradular cartilage in middle region of its dorsal inner surface; mt dorsal transversal muscle, or approximator muscle of cartilages, connecting dorsally both posterodorsal-lateral surfaces of cartilages, lying between superficial membrane that covers odontophore and tissue on middle region of radula; m4 pair of median dorsal tensor muscle of radula very large, thick, originating in ventral-middle-posterior region of odontophore cartilages, running towards medial, contouring medial-ventral surface of cartilages, running on their dorsal surface, inserting in subradular cartilage dorsal-posterior-medial extremities; m5 pair of median radular tensor muscle thick, originating in median-posterodorsal region of odontophore cartilages, near side of m2 insertion and m2a origin, covering perpendicularly m4 middle region, running medially, inserting along both sides of radular sac (each m5 branch covering a side of radular sac, medially and dorsally); m6 horizontal muscle very thin, uniting anterior half of odontophore cartilages, inserting on their dorsal margin; m7 pair of ventral tensor muscle of radula thin, narrow, originating inside radular sac ventral surface close to each other, running anteriorly, separating gradually from each other, inserting in radula ventral border; m8 pair of strong muscles originating in posterodorsal-lateral regions of odontophore cartilages near insertion of m2, running attached to dorsal margin of odontophore cartilages, inserting in their anterodorsal region close to horizontal muscle (m6); m9 pair of dorsal-medial tensor muscle of radula broad, thin, originating along dorsal-median surface of radular sac (in its region internal to odontophore), crossing to dorsal surface, inserting in dorsal-ventral border of subradular cartilage; mj jaws and peribuccal muscles somewhat thick, surrounding lateral and dorsal wall of buccal mass, originating around mouth, inserting in middle level of lateral and dorsal wall of odontophore; m11 pair of ventral tensor muscles of radula weakly present; m14 pair broad, thin, originating in posterodorsal region of odontophore, close to m2 and m5 origins, running towards ventral and anterior, inserting in snout inner ventral surface in about middle level of odontophore; tissue covering middle region of radula within odontophore, on its dorsal surface.

Radula short, little more than odontophore length (Figs. 29, 30); rachidian tooth narrow, strongly curved inwards, central cusp large, sharp, secondary cusps 2–4 similar-sized pairs (formula 2-1-2/0-0 to 4-1-4/0-0), weak pair of lateral reinforcements on its borders; lateral tooth broad (about three times broader than rachidian), curved inward, with about 7–10 short, triangular cusps, along edge on marginal side and 1-3 very weak cusps on edge on rachidian side, cusps decreasing laterally, disappearing about in middle region of tooth, with thick, arched border (formula from 1-1-7/0-0 to 3-1-10/0-0); inner marginal tooth long, curved, tall, tip sharply pointed (cusp formula 0-1-5/0-0 to 2-1-7/0-0); outer marginal tooth narrower than inner marginal tooth, thin, and with two small cusps along its inner margin only (cup formula 0-1-2/0-0 to 0-1-3/0-0).

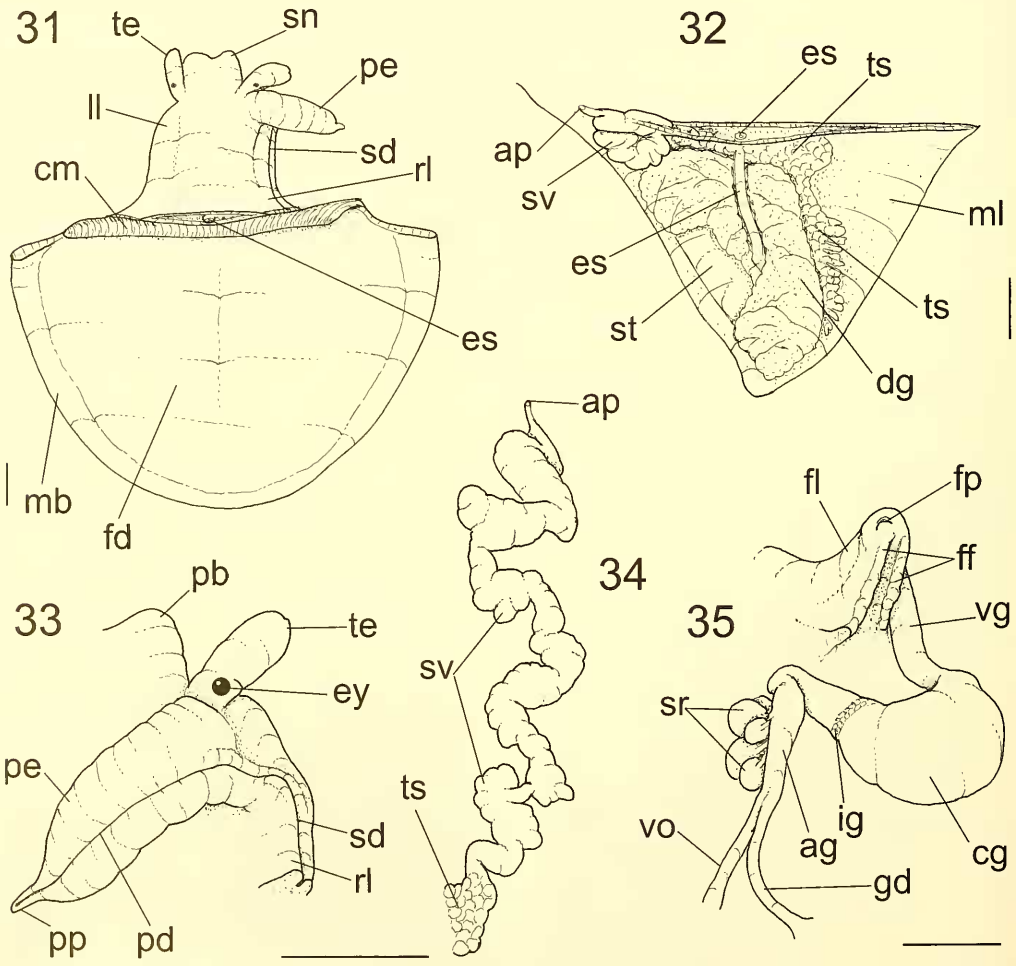
Pair of buccal ganglia large, close to each other near median line (Fig. 26: bg), located between buccal mass and adjacent esopha-



FIGS. 29, 30. Radula of *Crepidula cachimilla*. FIG. 29: General view of the radula. Scale bar = 100 µm. FIG. 30: Detail of the central and lateral tooth. Scale bar = 64 µm.

gus. Salivary glands not passing through nerve ring, longer than haemocoel, fitting inside it, bent (Figs. 18, 27: sg); distal end rounded, of about 1/3 of haemocoel width, running towards anterior possessing approximately same width along its length, narrowing close to buccal mass. Ducts of salivary glands broad, sinuous (Fig. 27: sa), running in dorsal surface of buccal mass, penetrating adjacent buccal mass wall a short distance, apertures small, in anterior region of dorsal folds of buccal mass.

Esophagus (Figs. 18, 28: es) narrow, long; anterior esophagus inner surface with pair of broad folds, running straight posteriorly, becoming gradually slender. Stomach (Fig. 28) somewhat conical, large, occupying about half of visceral mass size; esophagus inserting in left side of its posterior-left region, close to shell apex. Anterior duct to digestive gland located in region of stomach ventral surface preceding style sac, separated into two similar-sized, well-spaced ducts, each running in opposite directions, highly dichotomic. Posterior duct to digestive gland also duplicated (distance between this pair greater than that of anterior ducts), each one running in opposite direc-



FIGS. 31–35. *Crepidula cachimilla* anatomy. FIG. 31: Head-foot, male, dorsal view, pallial structures and visceral mass removed. FIG. 32: Visceral mass and adjacent part of pallial cavity, male, ventral view. FIG. 33: Penis and adjacent structures, dorsal view, penis deflected. FIG. 34: Visceral vas deferens extracted, seminal vesicle (sv) uncoiled. FIG. 35: Pallial oviduct, ventral view as in situ, most integument and pallial cover removed (except close to papilla). Scale bars = 1 mm.

tions, both very narrow, located in ventral region of stomach almost at its posterior end, one of them turned posteriorly.

Stomach gradually narrowing towards anterior and left, arriving close to left-posterior extremity of pallial cavity. Gastric shield occupying about 1/3 of stomach inner surface, located in its right side (Fig. 28: gs). Pair of longitudinal folds separating intestine from style sac running at left (Fig. 28: gf), in region anterior to anterior ducts to digestive glands, abruptly separating one another perpendicularly, in a T-fashion, surrounding entire stomach circumference in this region, forming a low, narrow fold separating style sac from main gastric chamber. A weak constriction marking region between style sac and main gastric chamber, clearer at right. Digestive gland pale brown in color, surrounding stomach except some areas on dorsal and ventral surfaces (Figs. 16, 20, 24). Intestine narrow, sinuous (Fig. 28: in), running on anterior border of visceral mass from left to right, initially in its ventral region, slightly near median line cross to its dorsal region and running up to right-anterior extremity of visceral mass (Fig. 28); running towards left in this region, becoming broader and exposed in pallial cavity, surrounding right and anterior border of kidney, abruptly running towards right in a U-shape, parallel to preceding loop (Figs. 16, 21, 28, 25: iu). Anus small, siphoned, located in right region of pallial cavity close to mantle border (Figs. 21, 28, 25). Final intestine loops filled with several small, elliptical fecal pellets.

Male Genital System (Figs. 31–34): Mature males up to 28 mm in shell length. Testis white, located mostly in anterior region of visceral mass (Fig. 32: ts). Sperm duct differentiable in region of testis just at right of esophagus penetration into visceral mass. Seminal vesicle intensely coiled, locally accumulated in anterior-right region of visceral mass (Fig. 32: sv); if uncoiled, presenting about same length as visceral mass; wall glandular, greatly irregular, varying from broad to very narrow along its length (Fig. 34). Seminal vesicle abruptly narrowing near pallial cavity, having a very narrow aperture located in right-posterior end of this cavity (Figs. 32, 34: ap). Pallial sperm groove starting immediately below this aperture, running as a relatively deep, narrow furrow with elevated edges. Pallial sperm groove running along right neck lobe close to its edge (Fig. 31: sd), slightly dorsal; abruptly curving towards left close to penis base, connecting to its posterior base region (Fig. 33). Penis located behind right cephalic tentacle, curved in same direction, of about 3–4 times its size (Fig. 31). Distal papilla long, about 1/4 of length of remaining penis region, about 1/5 of its width (Fig. 33). Penis groove deep, central, running along ventral surface up to penis papilla tip (Fig. 33).

Female Genital System: Ovary cream yellow, surrounding digestive gland, more concentrated in anterior region of visceral mass (Fig. 19: oy); when mature, oocytes distinguishable by their transparency. Visceral oviduct formed by gradual decrease from right-anterior end of ovary. Gonopericardial duct narrow, relatively short, originating in right-ventral extremity of pericardium, running ventral to visceral glands in area in which visceral mass encroaches toward pallial roof, inserting in posterior extremity of pallial oviduct, joined with insertion of visceral oviduct (Fig. 35: gd). Pallial oviduct narrow, located in right-anterior end of pallial cavity (Figs. 16, 20: ov). Seminal receptacles (sr) located in right side of last portion of visceral oviduct, four to five in number, with three always significantly larger (Fig. 35: sr); each a small sac; duct very narrow, long; their insertion preceding albumen gland, on right surface. Albumen gland long, narrow, whitish, its walls thick, glandular; located in anterior-right extremity of visceral mass, about half size of capsule gland (Fig. 35: ag). Separating albumen from capsule glands a narrow differentiable, paler colored tissue, most probably an ingesting gland (Fig. 35: ig). Capsule gland a continuation of albumen gland, but situated perpendicular and slightly dorsal to it, broad, spherical (Fig. 35: cg); walls thick glandular, pale brown; inner duct narrow, U-shaped, length about 1/8 of pallial cavity aperture. Vaginal duct (vg) relatively broad, equal in size to albumen gland. Genital pore preceded by tall, long papilla close to mantle border, at right and slightly removed from anus (Fig. 20: fl). Genital papilla with broader base and somewhat conical form; pair of well-spaced low folds running along its posterior-left side; both start gradually in papilla base and terminate at some distance from pore (Fig. 35: ff); posterior fold originating on surface of pallial cavity floor; anterior fold originating from pallial roof. Genital pore a transverse apical slit, perpendicular to papilla folds (Fig. 35: fp).

Reproduction

Animals categorized into four sexual phases: (1) undifferentiated juveniles, (2) males, (3) transitional individuals, and (4) females. These are easily recognizable under a microscope by observation of the external development of the reproductive organs. Juveniles are without visible sexual organs. Males have a well-developed penis. Transitional individuals have a penis in retraction phase and a developing genital papilla. Females lack a penis and have an easily distinguishable papilla.

Undifferentiated juveniles were between 3.7 and 5.1 mm SL (mean: 4.3 SD: 0.4 N: 11). Males were 5.4–28.5 mm SL (mean: 14.1 SD: 0.8 N: 103), always attached to larger individuals. Females were 9.6–52.2 mm SL (mean:

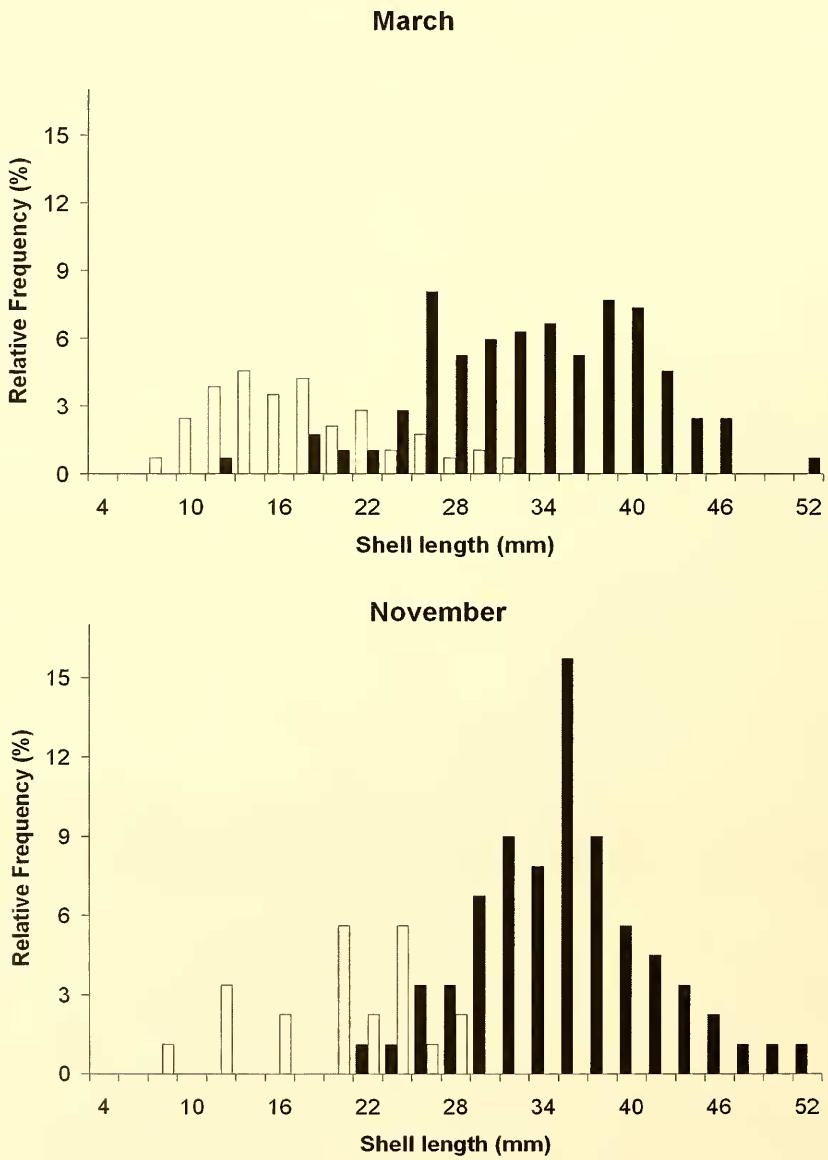


FIG. 36. *Crepidula cachimilla* sex proportion in March (N: 270) and November (N: 286). White: males; black: females.

37.3 SD: 0.9 N: 252), forming stacks of 2–5 individuals. The smallest brooding female was 23.5 mm SL; the largest was 49.5 mm SL.

Peak of female development from August to April (observed in 47 brooding females). Notable period of reproductive rest between March and November. No juveniles were encountered in the field during winter, being reflected in the diminution in the proportion of males in the population and their larger shell length in comparison with the summer (Fig. 36).

Egg masses with 15–65 capsules (Fig. 37) (mean: 35, SD: 14, N: 47). Egg capsules (Fig. 38) 2.2–3.3 mm in length (mean: 2.8, SD: 0.5, N: 148) and 2.3–3.4 mm in width (mean: 2.6, SD: 0.4, N: 148). Each egg capsule containing 129–441 uncleaved eggs (Fig. 39) (mean: 226, SD: 57, N: 148) in a whitish viscous liquid. All eggs developing into veliger larvae (Fig. 40) and hatching. It was not possible to measure hatching time. No nurse eggs or cannibalism was observed. No differences in number of embryos between initial and late brood stages in females of same size found.

Neither ln-transformed mean capsule size (r^2 = 0.01) nor ln-transformed capsule number per mass (r^2 = 0.13) correlated with shell length of brooding females. There was no positive correlation between ln-transformed egg number per capsule and ln-transformed capsule size (r^2 = 0.33) or ln-transformed female size (r^2 = 0.02).

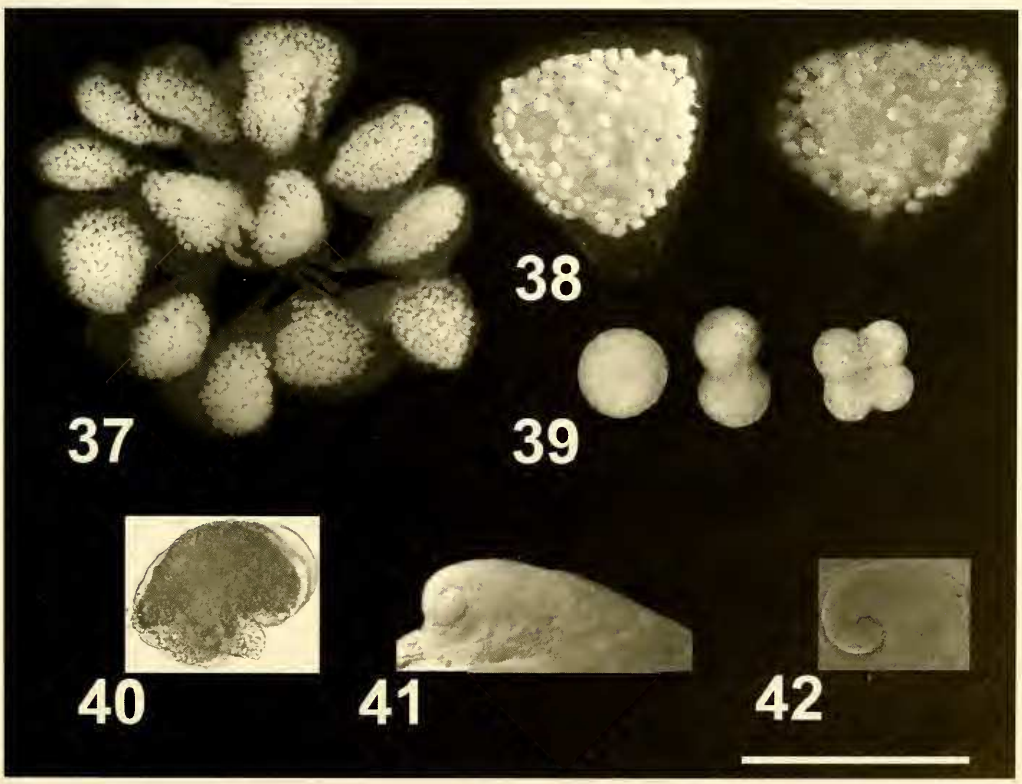
Uncleaved egg diameter 180–200 µm (mean: 191.7; SD: 7.2, N: 20). Protoconch length of juvenile shells (Figs. 41, 42) 700–800 µm (mean: 760 SD: 65 N: 11).

Habitat

Between 10 and 20 m depth, attached to hard substrata.

Distribution

Known only from northeastern Patagonia including the records from Golfo San Matías to Punta Norte of Parodiz (1939).



FIGS. 37–42. *Crepidula cachimilla* egg mass and protoconch. FIG. 37: Egg mass. Scale bar = 7 mm. FIG. 38: First and late stage egg capsule. Scale bar = 3.5 mm. FIG. 39: Eggs in first division stages. Scale bar = 500 µm. FIG. 40: Prehatching stage. Scale bar = 350 µm. FIG. 41: Protoconch on an adult shell. Scale bar = 800µm. FIG. 42: Detail with SEM of protoconch of an adult shell. Scale bar = 1,100 µm.

TABLE 2. Reproductive characteristics for *Crepidula* species from America compared with *C. cachimilla*.

Species	Reference regarding reproduction	Number of capsule per egg mass	Number of eggs per capsule	Uncleaved egg diameter (μm)	Nurse eggs
Crepidula onyx G. B. Sowerby I, 1824	Coe, 1942	50–100	100–200	no data	see discussion
C. onyx G. B. Sowerby I, 1824	Hoagland, 1986	19–60 (mean: 49)	100–300 (mean: 220)	160–180 (mean 172)	yes (6/capsule)
C. cachimilla	this study	15–65 (mean: 35 ± 14, N: 47)	129–563 (mean: 281 ± 74, N:148)	180–200 (mean: 191.7 ± 7.2, N: 20)	no
C. aplysioides Reeve, 1859	Miloslavich & Penchaszadeh, 2001	23 ± 5	3–12	300	no
C. coquimbensis Brown, 1996	Brown, 1996	-	62–135	195–263	-
C. dilatata Lamarck, 1811	Gallardo, 1977	22–29	308–1,016	-	yes
C. protea Orbigny, 1841	Hoagland, 1983	26–48	30–120	170	no
C. argentina Simone, Pastorino & Penchaszadeh, 2000	Cledon & Penchaszadeh, 2001	10–46	81–448	144–161	no
C. philippiana Gallardo, 1977	Gallardo, 1977	16–34	145–431	-	yes
C. fecunda Gallardo, 1977	Gallardo, 1977	-	mean 542	204–238	no
Bostrycapulus aculeatus (Gmelin, 1791)	Miloslavich et al., 2003	4–9 (mean: 9 ± 2, N: 51)	12–65 (mean: 38 ± 11, N: 57)	300–630 (mean: 417 ± 43, N: 263)	yes

(*continues*)

(*continued*)

Species	Hatching stage	Male shell length (mm)	Brooding female shell length (mm)	Maximum female shell length (mm)	Septum shape
Crepidula onyx G. B. Sowerby I, 1824	planktotrophic veliger larvae	4–30	-	60	-
C. onyx G. B. Sowerby I, 1824	veliger larvae	-	21–50	50	-
C. cachimilla	veliger larvae 260–300 µm	5.4–28.5	23.5–49	52.2	See shell description and figures
C. aplysioides Reeve, 1859	crawling juvenile 600 µm	-	9.4–18.2	-	-
C. coquimbensis Brown, 1996	crawling juvenile	-	-	-	S-shaped, apex never reaching margin
C. dilatata Lamarck, 1811	crawling juvenile	-	-	-	S-shaped, apex never reaching margin
C. protea Orbigny, 1841	veliger larvae	4.6–8.0	7.3–20	-	-
C. argentina Simone, Pastorino & Penchaszadeh, 2000	veliger larvae 190–230 µm	3.95–8.85	14.5–36	36	-
C. philippiana Gallardo, 1977	crawling	-	-	-	S-shaped, apex never reaching margin
C. fecunda Gallardo, 1977	-	-	-	-	S-shaped, apex never reaching margin
Bostrycapulus aculeatus (Gmelin, 1791)	4–20 crawling (mean: 13 ± 6, N: 5)	-	15–36	-	S-shaped, apex never reaching the margin

DISCUSSION

The shell of *Crepidula cachimilla* is similar to species occurring in the western Atlantic belonging to the "*Crepidula plana* complex" (Collin, 2000; Simone, submitted). Its most distinctive characters are the projecting apex, located somewhat away from the posterior shell base, and the absence of periostracum.

The characters of *Crepidula cachimilla* presented in the Diagnosis, mostly morphological, as well as those summarized in the Table 2, are the main basis differentiating this species. That set of characters easily separates the new species from the remaining South American taxa. From the Atlantic species with known anatomy, *C. cachimilla* has a thicker columellar muscle, a condition found only in other species in early stages of the development, after which the columellar muscle becomes reduced. As stated by Simone (2002), based on comparison of the ontogeny and phylogeny, the lateral and dorsal shell muscles are also derived from the columellar muscle, and are both thick in *C. cachimilla*; however, the respective scars in the shell are inconspicuous. The restriction of the pallial cavity aperture is one of the synapomorphies of the family Calyptraeidae (Simone, 2002); however, in *C. cachimilla* this state is still more developed, as it is greatly restricted on the right side by a broad fusion of the mantle border. The hypobranchial gland is normally reduced in *Crepidula*, being a thin glandular layer surrounding the visceral structures encroached into pallial cavity roof (Simone et al., 2000; Simone, 2002); however, *C. cachimilla* has practically no developed hypobranchial gland, the region where it would occur being thin and transparent. The contrary happens with the salivary glands, which are normally small; in *C. cachimilla*, these glands are longer than the haemocoel, being folded inside this cavity. This state is comparable with that of *Bostrycapulus aculeatus* (Gmelin, 1791) (also known as *Crepidula aculeata*); however, in that species, these glands are still larger (Simone, 2002). Other notable feature of *C. cachimilla* is the duplication of both ducts to digestive gland in the stomach.

Despite the conchological peculiarities of *C. cachimilla*, shell characters alone do not clearly distinguish it from *C. onyx*, which it resembles in shape, color, and size. This similarity led Parodiz (1939) to assume that the studied species was *C. onyx*. Such misidentifications are common in this family, with *C. argentina* (Simone et al., 2000) having been confused with *C. protea* in Argentina.

There are subtle differences in shell shape between *C. cachimilla* and *C. onyx*. *Crepidula cachimilla* tends to have a more pointed apex, and the shell also seems to be less convex, but these features can be strongly affected by the substratum.

Anatomical differences between *C. cachimilla* and *C. onyx* are not yet known, because there has not been a detailed anatomical study of the latter. However, the radular morphology of *C. onyx* (Hoagland, 1977) is markedly different from that of the studied species, in which the central tooth has 2–4 cusps (formula 2-1-2/0-0 to 4-1-4/0-0); the lateral tooth 7–10 cusps, (formula 7-1-0/0-0 to 10-1-0/0-0); and the inner marginal tooth has 1–3 cusps (1-1-0/0-0 to 3-1-0/0-0). In addition, the uncleaved eggs of the Argentinean material are larger than those of the Californian *C. onyx* population described by Hoagland (1986). The main difference between the species is the occurrence of six "malformed", or nurse eggs per sac (Hoagland, 1986) and the fact that "frequently fully half the entire number of embryos disintegrate within the capsules and are used as food by the survivors" (Coe, 1942). Although we are unable to assess the frequency of this phenomenon in California, such malformed eggs or disintegrating embryos were absent in the studied Argentinean material.

Aguirre & Farinati (2000) reported the presence of *C. onyx* among other *Crepidula* species from Quaternary sediments in Argentina. Because of the shell of the species described here is very similar to that of *C. onyx*, it is reasonable to assume that these fossil records belong to the species described here. The occurrence of these fossils proves that this is not an exotic species recently introduced to the area. Additional differences between the reproductive parameters reported by Hoagland (1986) and Coe (1942) for *C. onyx* and *C. cachimilla* are: the larger egg diameters and the complete lack of nurse eggs or cannibalism in *C. cachimilla*, and the different radular morphology. On this basis, the material studied by Parodiz (1939) should be assigned to the new species described here instead of being assigned to *C.* aplysioides, as proposed by Hoagland (1977).

Crepidula cachimilla also differs from other species in many reproductive strategy char-

acteristics. *Crepidula aplysioides* Reeve, 1859, is a small (up to 2.0 cm SL; brooding female between 9.4 and 18.2 mm SL) tropical and subtropical species with egg capsules containing fewer eggs than *C. cachimilla* (Hoagland, 1977). Further reproductive characteristics are given by Miloslavich & Penchaszadeh (2001). The number of eggs per capsule separates *C. cachimilla* from *C. coquimbensis* Brown & Olivares, 1996; *C. dilatata* Lamarck, 1822; and *C. protea* Orbigny, 1841 (Table 2). In *C. cachimilla* (Table 2), the egg diameter clearly differs from that of *C. argentina* (Cledón & Penchaszadeh, 2001), *C. philippiana* (Gallardo, 1977, 1996), *C. fecunda* (Gallardo, 1979) and *C. dilatata* (Gallardo, 1977; Chaparro & Paschke, 1990) (Table 2). In *C. cachimilla* (Table 2), eggs per capsule are more numerous, and both males and females are larger than those of *C. protea* (Hoagland, 1983). The larval shell at hatching and the protoconch of juveniles are larger in *C. cachimilla* (Table 2) than in *C. argentina* (Cledón & Penchaszadeh, 2001) (Table 2).

According to our observations on *C. cachimilla*, broods containing a large number of capsules (more than 40) always belong to females larger than 31 mm SL. Because of the number of eggs per capsule does not depend on the female size, we used this parameter as species representative.

A more extensive comparison of the morphology of *C. cachimilla* with other species of the "*Crepidula plana* complex" is being published elsewhere (Simone, submitted), with a phylogenetic analysis of all known species occurring from Florida to Patagonia. *Crepidula cachimilla* is separated from the remaining species by such plesiomorphies as the thickness of the shell muscles (columellar, lateral and dorsal muscles), which are very thin in the other species; the nephridial gland having clearly transverse septa, whereas in the remaining species this gland has irregular longitudinal folds; the larger size of the salivary glands, which are normally reduced; and retention of the ventral tensor muscle of the radula (m11), mostly lost in other species.

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